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On some population parameters of drosophilids in Switzerland (Diptera, Drosophilidae)

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Based on a collection of Drosophilidae in western Switzerland, the counts of flies were analyzed to get coordinated information about population parameters such as aggregation, succession, sex ratio, association and diurnal activity. The results are in conformity with data from literature.

Keywords: Population parameters, aggregation, succession, sex ratio, association, diurnal frequency.

INTRODUCTION

It is the general experience made by all collectors of drosophilids that sample size and species content vary in time and space, and in particular, that the method of collecting has an important influence on the result. Beside certain effects of chance, it has been shown that collecting by net sweeping and by baiting yields quite different results. This can be explained by the type and quality of the bait (e.g. Birch & Battaglia 1957; Johnston & Heed 1975; Beppu & Toda 1976; Atkinson 1977; Watabe et al. 1980; Atkinson 1981; McInnis 1981; Hoenigsberg *et al.* 1982; Sene *et al.* 1981; Carson & Heed 1983; Spence *et al.* 1984; Bächli *et al.* 1991; Mitsui & Kimura 2000), but mainly by characteristics of the habitat (e.g. Dobzhansky & Epling 1944; Crumpacker & Williams 1973; Sabath 1974; Toda 1974; Begon 1975; Shorrocks 1975; Atkinson & Shorrocks 1977; Begon & Shorrocks 1978; Taylor & Powell 1978; Atkinson & Miller 1980; Shorrocks & Nigro 1981; Begon 1982; Atkinson 1983; Bélo & Banzatto 1984; Shorrocks 1996).

The typical method for collecting drosophilids is using different kinds of baits which have provided information concerning various aspects, such as diurnal differences (e.g. Nozawa 1956; Wakahama *et al.* 1963; Hoenigsberg *et al.* 1977; Bélo & Lemos 1978; Rocha Pité 1978; Bächli *et al.* 1985; Argemí *et al.* 2000; Kravchenko et al. 2006), sex ratio differences (e.g. Mather 1956; Paik 1957; Burla 1961; Kaneko *et al.* 1966; Martin & Stevenson 1967; Kaneko *et al.* 1968; Hunter & Navarro 1969; Bächli 1973; Reddy & Krishnamurthy 1973; Begon *et al.* 1975; Toda 1976; Begon 1978; Bélo & Lemos 1978; McInnis *et al.* 1982; Gómez & Nájera 1987; Band 1993; Burla & Bächli 1993; Burla 1995; Argemí *et al.* 2002), associations of species, guilds (e.g. Watabe 1984; Shorrocks & Rosewell 1987; Shorrocks *et al.* 1990; Shorrocks & Sevenster 1995), aggregations (e.g. Shorrocks & Begon 1975; Shorrocks *et al.* 1979; Atkinson & Shorrocks 1984; Shorrocks & Rosewell 1988; Shorrocks 1990), successions of species (e.g. Bächli 1972; Atkinson 1977;

Bächli & Schatzmann 2006), niche characteristics (e.g. Hummel *et al.* 1979; Jaenike 1974; Shorrocks 1974) and other trends, e.g. influence of climatic factors (Stevenson & St. Clair 1953; Rocha Pité 1977) or absolute population size (Gromko 1981).

Because most of the reports mentioned are based on the different backgrounds of the respective projects, we have decided to combine in one study as many aspects as possible, in order to get information on some population parameters, giving a possibility to answer the following hypotheses:

— some species are aggregated over baits
— the aging process of the bait has an influence on the species composition
— males and females are differently distributed over baits
— some species are associated, forming a guild
— there are diurnal differences (morning/evening)

As it may be difficult to include several hypotheses in one study, we have tried to standardize the sampling procedures as well as possible, in order to avoid excessive effects of habitat choice of the involved species and other unwanted parameters. Anyway, it was not possible to evaluate the habitat structure etc. in detail; therefore, the following data are empirical and descriptive, and we were unable to provide a causal argumentation for the findings.

METHODS

Baiting

A collection of drosophilids was made by two of us (GB, EH) in the almost homogeneous, protected, extensive Scots Pine (*Pinus sylvestris*) woodland area Pfynwald, about 500 m above sea level, in the center of the canton Wallis, Switzerland, from August 2 to 5, 1999. In addition to the pine trees, occasionally a ground layer of certain bushes and herbaceous plants also existed (not recorded). As bait we used mashed, fermenting bananas put on the ground, in form of open plates. They were arranged in two parallel lines each of 10 plates in a distance of about 100 m, leaving in each line at least 10 m from plate to plate. The distance of the plates was considered large enough to provide as much independence of the individual bait as possible; we have to admit that this independence is not fully guaranteed.

The baits were brought out in the late morning of August 2. Collecting was made by net sweeping over the plates, beginning in the evening of August 2, then every morning and evening of August 3 to 5; on each occasion, the flies were sampled in three successive turns, allowing additional flies to be attracted and/or occasionally escaped flies to join the bait again.

During the collection time the weather conditions were favorable (warm, mostly sunny), but rather dry, to the effect that the bait suffered from an aging process, its condition changing successively from fresh bait to a compact, almost dried out version (with smell of acetic acid), with an obvious loss of attraction capabilities. The baits were slightly irrigated on August 4.

The flies were immediately identified and afterwards stored in ethanol.

Tab. 1. Overview. Counts per species and day and daytime, including some population parameters.

	August:	2	3	3	4	4	5	5	
	Daytime:	E	M	E	M	E	M	E	
Species	Code								Totals
Amiota alboguttata	AG							1	1
Chymomyza amoena	AO				2			1	3
Drosophila ambigua	AM				1		1		2
Drosophila funebris	FU				1	1			2
Drosophila helvetica	HE		2	8	23	34	22	5	94
Drosophila hydei	HY	1		3	1	2			7
Drosophila immigrans	IM		7	8	27	21	11	5	79
Drosophila kuntzei	KU	2	107	191	387	248	459	209	1603
Drosophila limbata	LI					1		1	2
Drosophila littoralis	LT	1	15	21	30	44	35	7	153
Drosophila melanogaster	ME	14	41	167	61	67	9	28	387
Drosophila obscura	OB		84	20	104	38	82	9	337
Drosophila phalerata	PH		104	93	227	94	338	109	965
Drosophila subobscura	SO	30	521	516	552	675	281	170	2745
Drosophila testacea	TE		305	345	981	574	1123	581	3909
Drosophila transversa	TR	1	45	19	74	58	92	47	336
Drosophila tristis	TT		1	1	8	4	4		18
Leucophenga maculata	MA		1		2				3
Lordiphosa fenestrarum	FE					1			1
Phortica semivirgo	SE		1				3	1	5
Scaptodrosophila rufifrons	RU			1		1		2	4
Scaptomyza pallida	PA	1		3		3	1	4	12
Totals		50	1234	1396	2481	1866	2461	1180	10668
Number of Species		7	13	14	16	17	14	16	22
Indices:									
Diversity H'		1.59	2.39	2.45	2.49	2.47	2.31	2.22	2.51
EXP (H')		3.02	5.25	5.46	5.61	5.55	4.95	4.66	5.68
Simpson's D		0.56	0.74	0.76	0.08	0.75	0.72	0.69	0.76
Equitability		0.57	0.65	0.64	0.62	0.61	0.61	0.55	0.56

Data analysis

Parameters

For some population parameters, the indices mentioned by Bächli & Schatzmann (2006) were calculated.

Statistics

The aim of the study was to investigate the distribution of drosophilid flies over similar baits over a few days. The design led to 3 evaluable days with 2 daytimes each, morning and evening, and 20 baits. The baits can be seen as not fully independent repetitions.

Most analyses were applied on the square roots of the original counts. This is a widely used transformation applied on count data (e.g. Osborne 2002).

Only the data of August 3, 4 and 5 were statistically evaluated. On August 2 there was a test run to examine whether the location of the baits was suitable. This

Tab. 2. Dispersion of species. Mean, variance and dispersion index DI over the 20 baits were calculated per day, daytime, species and sex; weighted mean values of these three statistics are shown in the table. Accumulations are expressed by a DI > 1. All species but *S. pallida* show an aggregated distribution.

Species	Flies	Mean m	Mean var	Mean DI
D. helvetica	94	0.84	1.81	2.1
D. immigrans	79	0.51	0.64	1.2
D. kuntzei	1,601	10.16	155.92	12.9
D. littoralis	152	0.95	3.48	3.0
D. melanogaster	373	2.71	8.40	2.6
D. obscura	337	2.23	5.49	2.1
D. phalerata	965	6.41	48.05	7.7
D. subobscura	2,715	13.90	128.97	8.5
D. testacea	3,909	22.20	249.54	10.2
D. transversa	335	2.08	5.30	2.2
D. tristis	18	0.22	0.43	1.6
S. pallida	11	0.10	0.09	1.0
All 22 species	10,618	14.10	153.43	8.9

test run is included in Tab. 1, but is excluded from any further statistical analysis, because it is not systematically comparable with the other days.

Principally, species with less than 10 individuals in the total are omitted from analysis.

All statistical analysis was performed with SAS (Version 6.12). Van Elteren's test was performed with the procedure FREQ and options «cmh2» and «scores=modridit». All tests were performed without correction for multiple testing and are to be interpreted as descriptive.

Similarities of distributions were measured with the similarity index τ developed by Schatzmann (1986), as this index has proved to be biologically correct and largely independent of varying sample sizes. The formulae for calculating this similarity (without correction for sampling intensity) are:

$$\frac{2\hat{\tau}_1}{2-\hat{\tau}_2+\hat{\tau}_1} = \hat{\tau}$$

with

$$2\sum_i \frac{p_i q_i}{p_i + q_i - \frac{N_x + N_y}{2N_x N_y}} = \hat{\tau}_1$$

and

$$2 - \sum_i\left[\left(\frac{1}{p_i} + \frac{q_i(N_x-1)}{p_i(x_i-1)}\right)^{-1} + \left(\frac{1}{q_i} + \frac{p_i(N_y-1)}{q_i(y_i-1)}\right)^{-1}\right] = \hat{\tau}_2$$

where

i = sampling unit

x_i resp. y_i = observed number of individuals of species X resp. Y in unit i

$N_x = \sum x_i$; $N_y = \sum y_i$

p_i resp. q_i = observed frequency of species X resp. Y in unit i; $\sum p_i = 1$; $\sum q_i = 1$

Tab. 3. Totals of square root transformed counts of specimens of the 12 most abundant species at each of the 20 baits. The baits had a comparable attraction of flies. However, the baits were not independent of each other.

Bait number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	All
Species																					
D. helvetica	0	1	2	2	4	2	0	3	3	7	3	3	2	2	1	0	6	6	10	7	65
D. immigrans	1	0	1	2	3	5	1	0	9	2	7	4	1	1	2	4	4	7	7	5	67
D. kuntzei	52	52	21	19	30	20	23	33	54	9	27	12	13	6	6	5	11	17	25	32	469
D. littoralis	1	2	1	6	11	6	2	4	18	4	6	1	1	2	4	5	4	9	7	8	103
D. melanogaster	1	1	3	8	12	11	7	9	21	8	17	5	22	8	8	6	16	14	17	11	205
D. obscura	6	11	7	13	13	13	6	6	13	12	17	5	8	6	2	4	11	15	17	11	197
D. phalerata	25	40	15	18	28	18	17	29	38	12	17	13	9	7	3	6	13	15	19	21	362
D. subobscura	15	30	28	38	43	33	19	23	23	47	39	35	39	34	32	30	50	52	58	42	711
D. testacea	49	60	37	38	49	38	41	51	73	35	43	40	27	22	21	22	40	52	58	59	854
D. transversa	15	17	13	13	14	8	11	12	14	16	5	9	8	6	7	8	7	8	8	10	207
D. tristis	0	0	0	0	0	0	0	1	0	3	4	0	0	0	0	0	1	3	3	0	15
S. pallida	0	0	0	2	0	3	3	0	0	2	0	0	0	0	0	0	0	0	0	1	11
All	165	215	129	158	207	157	130	172	266	158	184	127	130	94	87	90	163	198	230	207	3266

Similarities were visualized with the procedure MDS, with the option «similar». Principal component analysis was performed with the procedure PRINCOMP, with default options. Additional explanations are given where appropriate below.

RESULTS

Overview

The daily results of the morning and evening collections are summarized in Tab. 1. That the results of the first and the last day differ from the other samples is caused by the respective condition of the bait. The total is dominated by *D. testacea* von Roser, a fungivorous species, and *D. subobscura* Collin, an omnipresent species, to a lower degree by the fungivorous species *D. kuntzei* Duda, *D. phalerata* Meigen and *D. transversa* Fallén. The domestic species *D. funebris* Fabricius, and *D. hydei* Sturtevant were rather rare, however, *D. melanogaster* Meigen and *D. immigrans* Sturtevant were well represented; we believe that an adjoining restaurant and a farm may have some influence on the local fauna. The presence of many specimens of *D. littoralis* Meigen may depend on the river Rhone (Rotten) flowing along the woodland area in a distance of about 250 m from the collection site. The population indices are rather stable across all collections except for the first one.

Hypotheses

Species are aggregated over baits

Mean number of flies m, variance var and dispersion index DI = relation of variance to mean were determined for each collection over the 20 baits per day, day time, species and sex. Tab. 2 shows the weighted means of these statistics, where m was used as weight.

We use here the dispersion index DI as a measure of aggregation. As expressed by the mean DI, *D. immigrans* showed the weakest aggregation, *D. kuntzei* the strongest one, followed by *D. subobscura* and *D. phalerata*; the mean DI of the latter species is already below the value for all 22 species.

As the square root transformation is commonly used for count data, we have decided to base all further analyses on the square root transformed counts per day, day time, bait, species and sex. We think that by this transformation the aggrega-

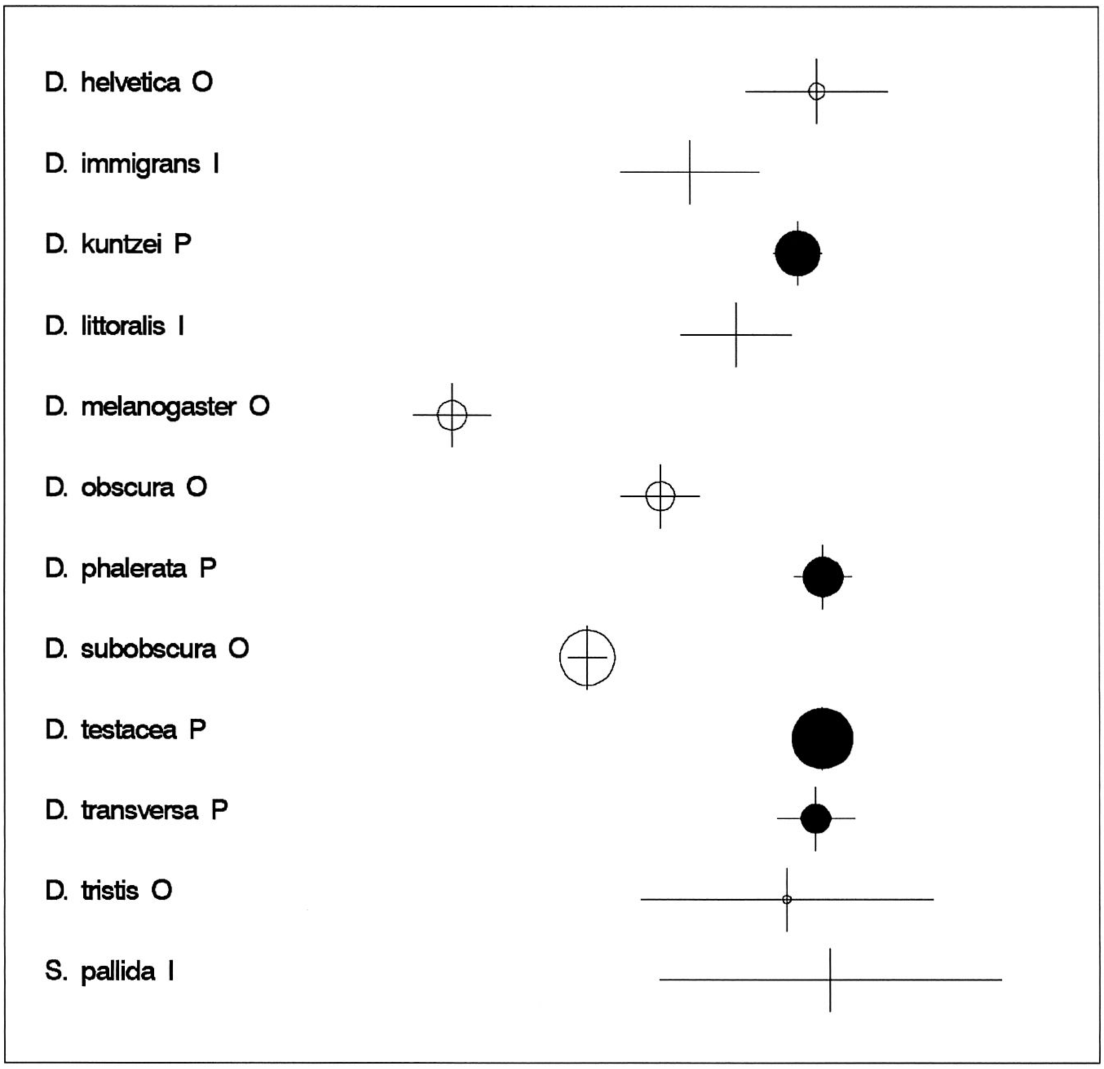


Fig. 1. Mean ranks of daily appearance of species. Letters after the names mean O= frugivores, P = fungivores, I = indifferent species; vertical line = mean day score, horizontal line = mean day score ± standard deviation. Circles: black = fungivore, white = frugivore, with the area proportional to the square root transformed number of flies. The typical appearances by species are evident. Frugivores appear before fungivores.

tion of the flies is sufficiently reduced to make the following analyses and conclusions valid. Tab. 3 shows the totals of the transformed counts by bait and species.

Frugivorous species appear before fungivorous species

As observed by Bächli & Schatzmann (2006), fresh, strongly fermenting baits attract frugivorous species, whereas older baits due to progressive fermentation, an aging process, are more attractive for fungivorous species. To test this hypothesis we compared the ordered distribution of the square root transformed counts of the two categories frugivorous and fungivorous flies over the 3 days with the Mann-Whitney-U-test. Average scores were used for ties. The following 3 categories of species were distinguished: frugivores: *D. helvetica*, *D. melanogaster*, *D. obscura*,

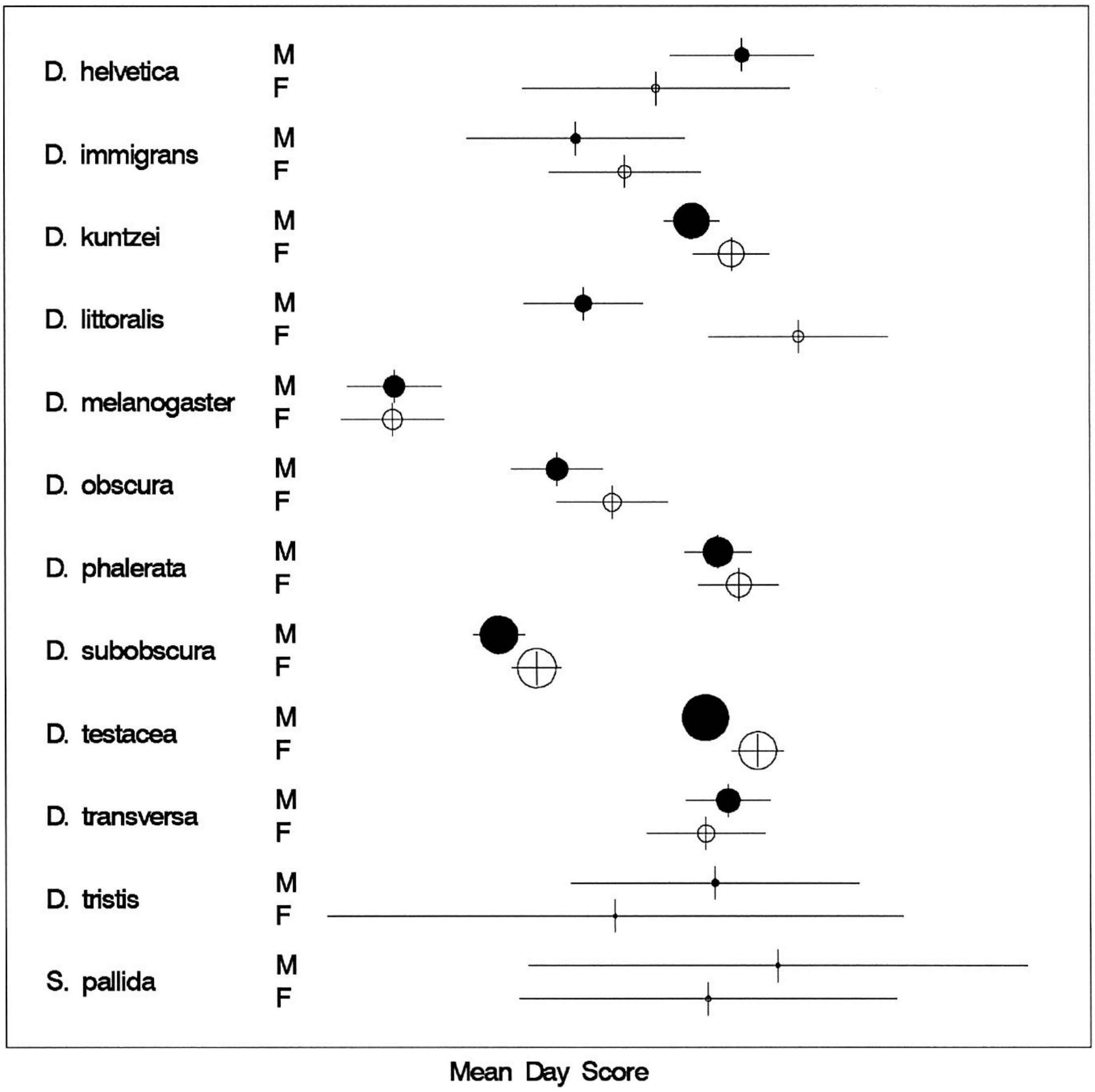


Fig. 2. Ranks of daily appearance of sexes by species. Vertical line = mean day score, horizontal line = mean day score ± standard deviation, thus marking the uncertainty. Circles: black = male, white = female, with the area proportional to the square root transformed number of flies. In general, males appear earlier than females.

D. subobscura, *D. tristis*; fungivores: *D. kuntzei*, *D. phalerata*, *D. testacea*, *D. transversa*; indifferent species: *D. immigrans*, *D. littoralis*, *S. pallida*. Indifferent species were excluded from this test.

The test confirmes that frugivores appear before fungivores with high significance ($p < 0.0001$, one sided and two sided). However, this test is dominated by the two most abundant species, *D. subobscura* and *D. testacea*. A more differentiating overview may be gained from Fig. 1 which shows mean Wilcoxon scores of the day of capture.

The figure clearly shows that in general white symbols are placed more to the left than black ones, which confirmes our hypothesis that frugivores appear sooner than fungivores. An exception may be *D. helvetica* whose mean score estimate, however, is not too precise.

Tab. 4. Proportion of males in the square root transformed counts of the 12 most abundant species, with 95 % confidence limits (CL). In general, males were more abundant than females; in *D. immigrans*, females were more abundant. For *D. melanogaster*, *D. subobscura* and *S. pallida*, the departures from 1:1 are not significant.

Species	number of flies	numbers transformed	% males	95%-CL
D. helvetica	94	65	0.769	65%-86%
D. immigrans	79	67	0.328	22%-45%
D. kuntzei	1601	469	0.648	60%-69%
D. littoralis	152	104	0.683	58%-77%
D. melanogaster	373	205	0.541	47%-61%
D. obscura	337	197	0.589	52%-66%
D. phalerata	965	362	0.586	53%-64%
D. subobscura	2715	711	0.482	45%-52%
D. testacea	3909	854	0.596	56%-63%
D. transversa	335	207	0.657	59%-72%
D. tristis	18	15	0.8	52%-96%
S. pallida	11	11	0.364	11%-69%

Males appear before females

According to our experience males appear before females. We tested this hypothesis with the stratified Wilcoxon test, also known as van Elteren test or Cochran-Mantel-Haenszel row-mean test, with only 1 degree of freedom, with day ranked and species stratified. It turned out that males appear significantly earlier than females ($p = 0.051$, 2-sided). Fig. 2 confirms this for the majority of species. However, for *D. helvetica*, *D. transversa* and *D. tristis* it seems that females appear first. Also *D. melanogaster* does not support any sexual difference in attraction by the baits.

Sex ratio and distribution of males and females over baits

For the 12 most abundant species, we have calculated the proportion of males and confidence limits based on binomial distributions (Tab. 4). The sex ratio was not significantly different from 1:1 at the 5 % level for *D. melanogaster*, *D. subobscura* and *S. pallida*, as their confidence limits do not include 50%. In general, males were distinctly more abundant than females. For *D. immigrans* males are significantly less abundant than females.

If females appear after the males at the baits, then it might well be possible that the females don't split on the baits in the same way as the males do. But the Cochran-Mantel-Haenszel-test with 19 degrees of freedom, stratified by species, doesn't indicate any difference in the distribution between males and females over the baits ($p= 0.51$).

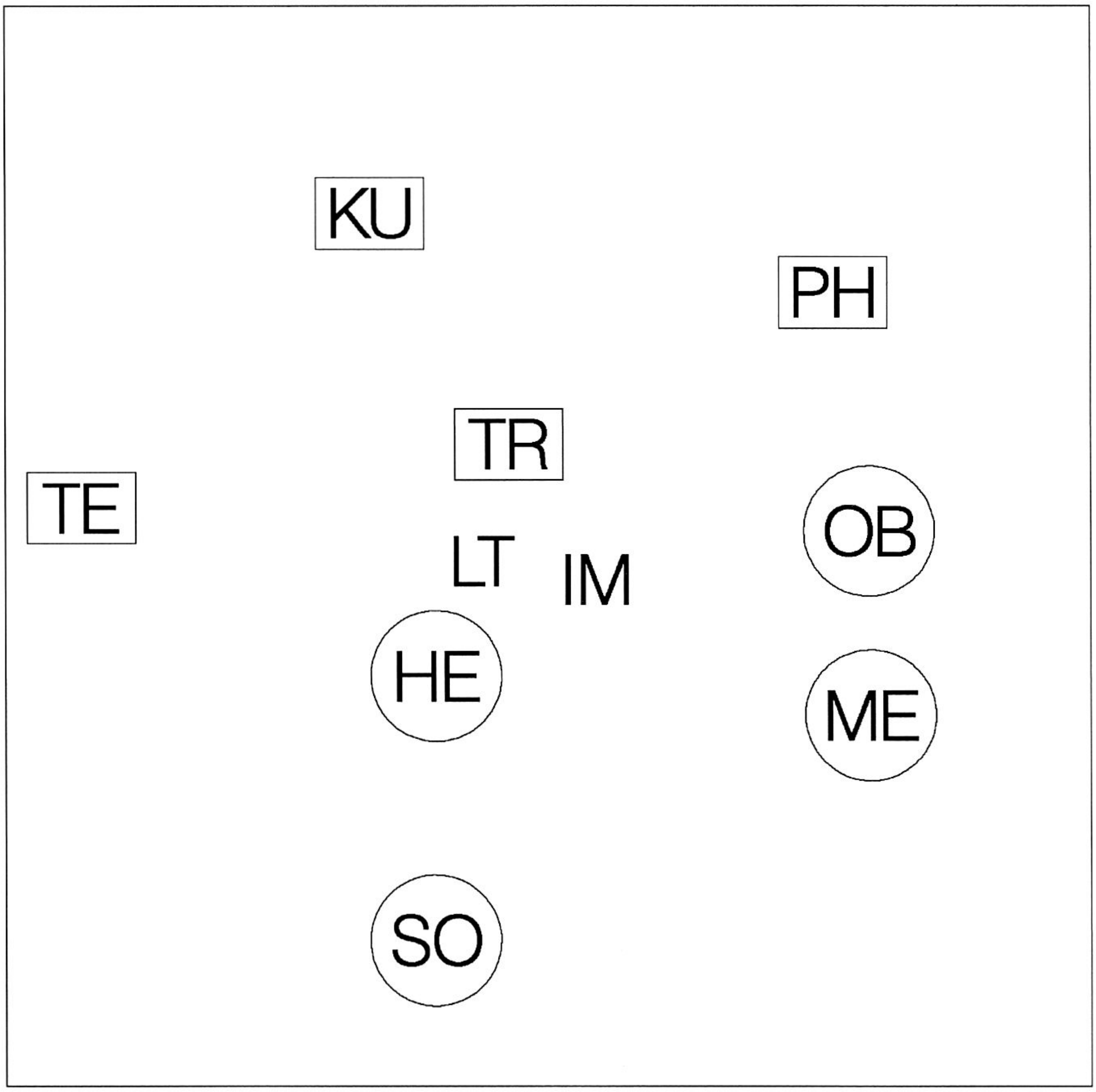


Fig. 3. Association of species in respect of day, daytime and bait. *D. tristis* and *S. pallida* were omitted from this kind of analysis due to their small quantity. Species codes according to Tab. 1. Circles = frugivores, rectangles = fungivores. The ecological grouping is visible but not very clear. Frugivores and fungivores are clearly separated, but there are no further plausible groupings.

Some species are associated, forming a guild

As there was only one habitat, it was not possible to investigate associations to habitat with the underlying data. But associations between species were analyzed in respect of day, day time and bait. The associations were measured with the similarity index developed by Schatzmann (1986) on the square root transformed counts of flies. The similarity matrix was then visualized in Fig. 3 by multidimensional scaling.

Frugivorous and fungivorous species are clearly separated guilds, but not nicely grouped. Further plausible guilds are not recognizable. If any two species would have a tendency to meet on the same baits then this should show up in this representation. This analysis supports the results of the analysis of the succession

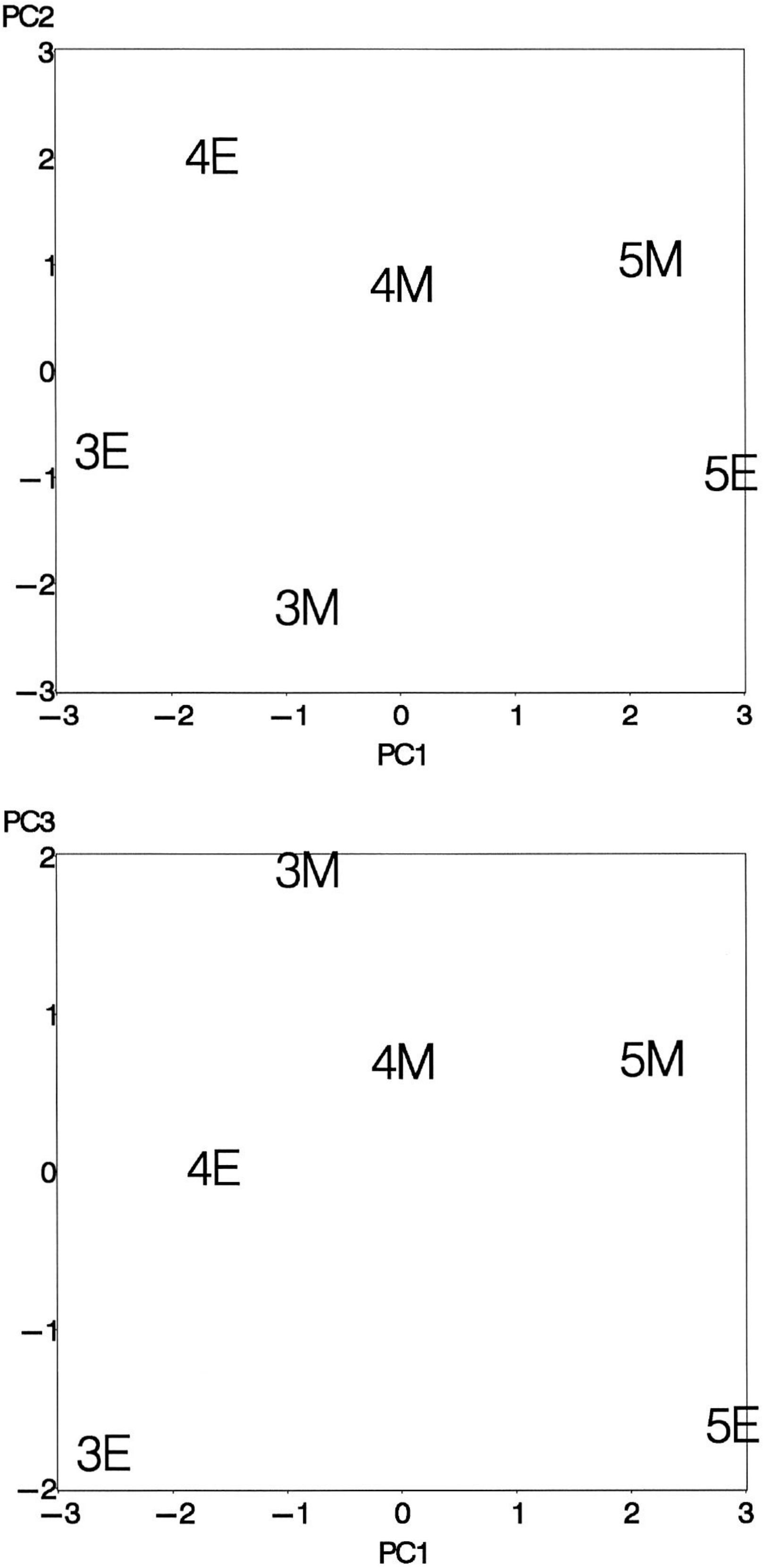


Fig. 4. First 3 principal components of faunas per day and daytime. Numbers 3 to 5 indicate the day of capture, letters M and E stand for Morning and Evening, respectively. Day of capture, i. e. age of bait, increases with PC1 and PC2 in the diagonal from bottom left to top right. The third principal component PC3 goes along with the day time; morning catches are positioned in the upper part, evening catches in the lower part.

of species due to the aging of the baits, but it does not reveal any further clear association or segregation. This might be due to the lack of some suitable hypotheses.

There are diurnal differences (morning/evening)

The following analysis arranges the 6 catches of the 3 days and 2 daytimes according to the composition of the 10 most abundant species caught. The relative contributions of the square root transformed counts of each species to the total size of the catch were analysed with a principal component analysis. The resulting first two principal components PC1 and PC2 contain 71 % of the original information, the third principal component PC3 does contain another 21 %. The results are shown in Fig. 4 with the catches and in Fig. 5 with the main focus of the species. Each figure is divided into two parts which are thought to belong together to form a cube. PC1 and PC2 seem to be related with the day of capture, i.e. the age of the baits, which increases with both of them, whereas PC3 best separates mornings from evenings (Fig. 4).

Fig. 5 shows the placement of the species according to their loadings on the first three principal components. Frugivorous species (SO, ME, OB, HE) are placed on the left of PC1, fungivores on the right (KU, TE, PH, TR). The two indifferent species *D. littoralis* (LT) and *D. immigrans* (IM) are similarly distributed over the catches. These two species and *D. helvetica* have the highest loadings on PC2 and are also the least frequent species in this analysis; therefore PC2 could somehow still be related to the overall frequency of the species, although the analysis was based on relative frequencies. PC3 finally shows species like *D. obscura* (OB) which were caught mainly in the morning at the top, and species from the evening at negative values of PC3. The inspection of the daily ratios of the morning and evening counts in Tab. 5 for *D. melanogaster* and *D. obscura* or *D. phalerata* clearly confirms this phenomenon.

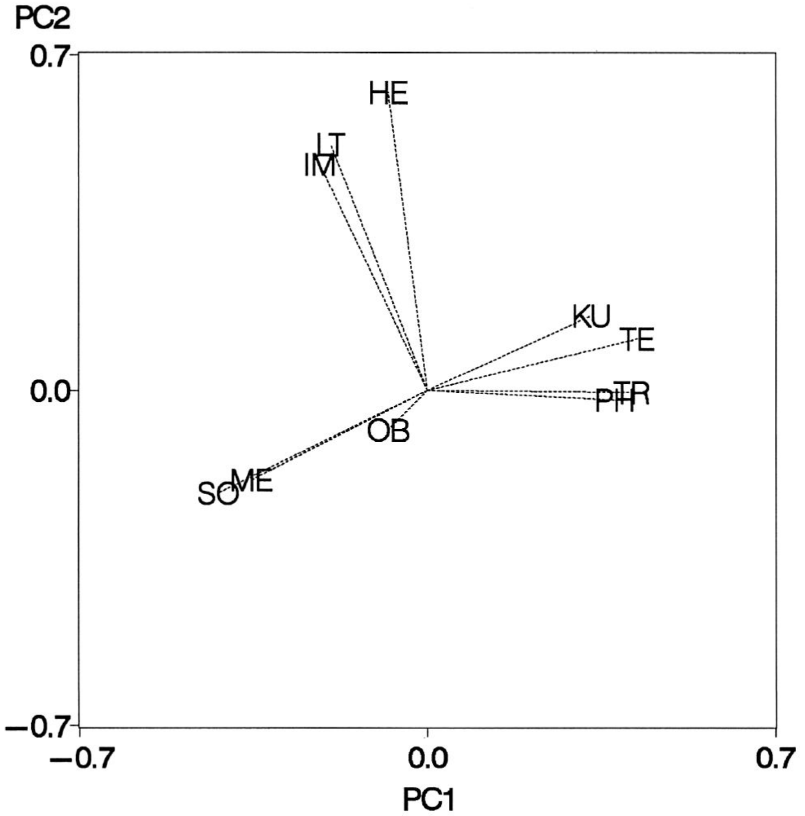
DISCUSSION

Overview

More than 20 years earlier, a study of the vertical distribution of drosophilids along a mountain slope was undertaken (Bächli 1979). The lowest collection site was not far from the present one, along the forest edge close to the river Rhone (Rotten). A total of 4211 flies of 16 species were recorded, dominated by *D. subobscura*, *D. testacea*, *D. transversa*, *D. obscura* and *D. phalerata*, whereas the number of *D. kuntzei* was much smaller.

Some species occur at low frequency in our collection, which may be due to the fact that they are rare (Birch & Battaglia 1957) or, more probably, be an effect of the collecting method, as species like *D. fenestrarum* and *Phortica semivirgo* are not particularly attracted by a fermenting bait, but occasionally caught by net sweeping (Beppu & Toda 1976; Disney *et al.* 1982).

Some authors have emphasized that the number and arrangement of the baits may have some influence on the number of flies collected (e.g. McInnis 1981; Sene *et al.* 1982). Our arrangement of the baits, in view of their distance and the homogeneity of the environment, was decided to minimize such effects. However, we



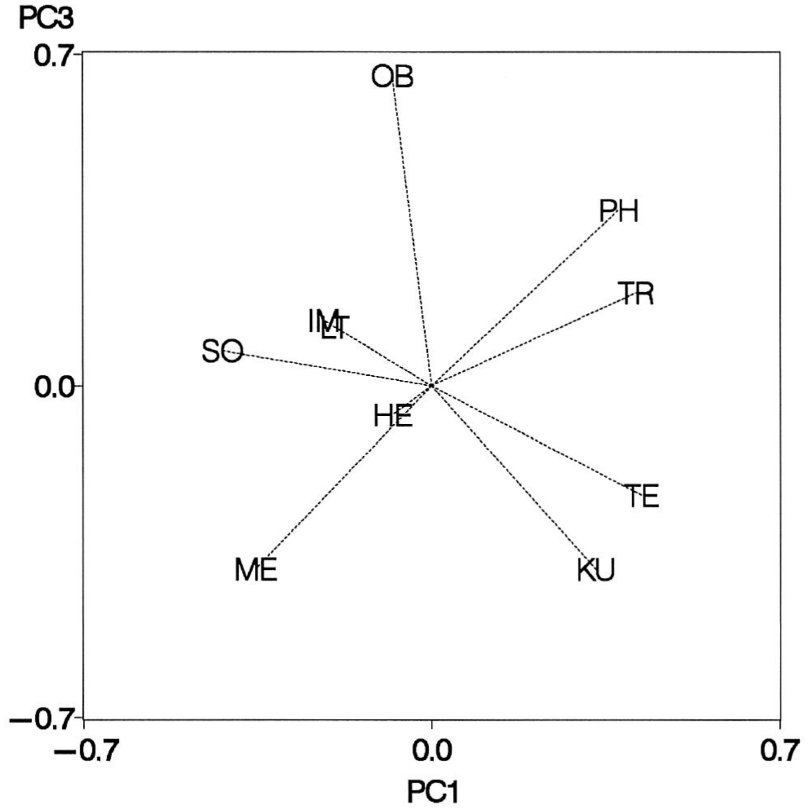


Fig. 5. Loadings of species on the first 3 principal components of faunas. Species codes according to Tab. 1. As in Fig. 4, the diagonal from bottom left of PC1 and PC2 to top right represents the days or the degree of aging of the bait; frugivores are on the left, fungivores on the right. PC3 from top to bottom represents the daytime. Therefore, *D. obscura* appeared mainly in the morning, *D. melanogaster* in the evening on fresh fermenting baits, *D. kuntzei* in evenings on more aged baits.

Tab. 5. Counts after square root transformation per bait and sex. M = morning, E = evening. Symbols: # = frugivorous species; * = fungivorous species. *D. obscura* was caught mainly in the mornings, *D. melanogaster* mainly in the evenings.

	October:	3	3	4	4	5	5	
	Daytime:	M	E	M	E	M	E	All
	Species							
#	*D. helvetica*	1.4	7.4	15.4	21.1	15.5	4.4	65.3
	D. immigrans	6.4	8.0	20.2	17.4	10.4	4.4	66.8
*	*D. kuntzei*	46.5	66.7	102.8	73.0	112.3	67.6	468.9
	D. littoralis	10.5	14.8	21.6	24.6	25.1	6.4	103.0
#	*D. melanogaster*	27.5	70.2	39.5	38.6	9.0	20.3	205.1
#	*D. obscura*	44.6	17.0	55.9	27.4	46.1	6.4	197.5
*	*D. phalerata*	54.0	30.8	81.0	48.3	101.2	46.5	361.9
#	*D. subobscura*	130.5	132.0	137.9	151.8	96.1	62.4	710.6
*	*D. testacea*	92.3	96.8	183.5	143.0	198.9	139.2	853.7
*	*D. transversa*	29.6	16.7	44.9	35.0	48.6	32.2	207.0
#	*D. tristis*	1.0	1.0	6.0	3.4	4.0	0	15.4
	S. pallida	0	3.0	0	3.0	1.0	4.0	11.0
	All 12 species	446.3	468.4	715.7	592.7	672.1	399.9	3295.1

suppose that the individual baits may be too close together to be independent enough, but we do not quantify such factors.

Aggregation

That some species are aggregated has been shown by several authors, in part by laboratory tests and simulations. Shorrocks (1990) reviewed the known facts and argued, that a plausible explanation is related to preventing competition between species.

We do not know what kind of and how many natural resources are available in the area studied. We can at least consider that the 20 baits used provide a large amount of food for many drosophilid species (and for some other insects as well). The baits are attractive enough for most of the involved drosophilids in the area and large enough as food resources. Therefore, there is no obvious reason for competition and we conclude that aggregation of species is not an important behavioral aspect.

Our reviewer did not fully agree with us about how we applied the square root transformation for reducing the aggregation. But we believe that this transformation or similar ones or even a negative binomial model play exactly this role, to reduce the raw counts at the sampling units which are inflated by common breeding sites, common attractors etc. to the counts of the very original, independent events. After such a reduction of aggregation we think that it is allowed to apply statistical methods which presuppose independent events, with some caution. Even for calculating the proportion of males of the 12 most abundant species we calculated the confidence ranges based on binomial distributions of rounded square root transformed count data. If we would apply the same methods on the raw counts, then a bulk of males – remember: males appear first – could distort the calculations more than these statistical methods presuppose, and the calculated confidence range would be misleadingly too narrow. We think that by using the square root transformed counts for our analysis we are even a bit conservative in the interpretation of our data.

Sequence of attraction

That the composition of the species collected changes with the age of the bait was mentioned by several authors (e.g. Bächli & Schatzmann 2006). Atkinson (1977) made a detailed study of some drosophilid species attracted in relation to age and decomposition of bananas over a period of 7 weeks. By using fermented bananas, the aging process of the bait is much faster; during Swiss summer climatic conditions the bait is almost fully decomposed after about 7 days. In our study, there is an additional effect: the dry climate of central Wallis forced the baits to dry out and, without our watering them, the attraction for most species is supposed to drop much sooner than normal. Anyway, the decrease of attraction of ecologically different species, conventionally interpreted as succession by us, has clearly been shown.

Sex ratio

We suppose that the sex ratio of the species collected may be influenced by at least two main factors: 1) the aggregation of the sexes on certain baits is different: males are accumulated; 2) the collecting method was unsufficient: the sexes react differently when disturbed by net sweeping, the escape behavior could be jumping or hiding, different by sex. At least, one can imagine that the large, well fed and/or pregnant females do not leave the bait and, therefore, are not caught by the net moving above the bait. Other factors may be: temperature and other climatic influences, kind of baits, behavioral characteristics, etc.

That males may outnumber females has been recorded by many authors (e.g. Paik 1957; Martin & Stevenson 1967; Gómez & Nájera 1987; Burla 1995). In most of the reported cases, there are exceptions in certain species, and clearcut reasons were not fixed.

For many species, it has been shown that females are concentrated at resources suitable for egg-laying. On the other hand, males and females are looking for feeding resources, and, therefore, may occur in common on such substrates. Males may stay (and accumulate) on feeding resources, waiting for females frequenting there and then trying to mate. In many species, males display at selected places (lek behavior, e.g. Grossfield 1978). We cannot exclude that such effects have occurred on our baits as well.

Associations, guilds

As mentioned by Shorrocks & Rosewell (1987), drosophilids may behave as guilds, comprising several species with similar ecological backgrounds, in particular having almost the same feeding and/or breeding behavior. In our analysis, we can separate two such associations, both containing the same species as already grouped based on our succession analysis. As shown by Shorrocks & Rosewell

(1987) the size of such guilds may be much larger, containing up to 26 species in tropical areas. The small size of the guilds observed by us depends on the number of locally existing species and also of their abundance allowing the analysis.

Diurnal differences

It is a common experience that most of the drosophild species living in the temperate zones show two main activity periods, one in the morning soon after sunrise, the other in the evening, almost ending at sunset. That the solar light intensity and the population dynamics are closely related has already been demonstrated (e.g. Argemí *et al.* 2000; Kravchenko *et al.* 2006). To be effective, collections are carried out during these daytimes. One can suppose that the species are identically active during both main activity times; however, as we have shown in our data, there are some diurnal differences which are superimposed by other factors. We were unable to see a clear trend, but some authors have shown that the morning activity was more intensive (e.g. Bächli *et al.* 1985), others that the evening activity was dominant, at least in some species (e.g. Argemí *et al.* 2000).

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ZUSAMMENFASSUNG

Wir sammelten Drosophiliden im Pfynwald (Mittelwallis) mit Bananenködern, die so ausgelegt waren, dass Informationen über einige Populationsparameter gewonnen werden konnten: Aggregation, Sukzession, Geschlechtsverhältnis, Assoziation und das tägliche Aktivitätsmuster.

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